

Apple powdery mildew caused by *Podosphaera leucotricha*: some aspects of biology

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Summary: Apple powdery mildew (*Podosphaera leucotricha*) occurs wherever apples are grown. One of the most important fungal disease of apple which causing severe economic loss on susceptible apple cultivars. Biology of the pathogen is widely investigated all over the world in the past 100 years. In this review, a summary from this enormous research is made for biology of apple powdery mildew in the following aspects: geographical distribution, morphology, taxonomy of the causal agent, symptoms, host susceptibility, resistance durability and disease cycle.

Key words: *Malus x domestica* Bork., apple powdery mildew, *Podosphaera leucotricha*, geographical distribution, symptoms, host susceptibility, disease cycle, biology

Introduction

Apple powdery mildew (*Podosphaera leucotricha*) is a worldwide known fungal pathogen of apple. A key important fungal disease of apple which causing severe economic loss on susceptible cultivars in every years where apple are grown (Hickey & Yoder, 1990). Biology of the pathogen is widely investigated all over the world in the past 100 years. Thousands of publications were aimed to investigate the pathogen features and to understand biology of this disease in order to improve powdery mildew forecasting and disease management. The aim of this review was to prepare a summary for biology of apple powdery mildew including geographical distribution, morphology, taxonomy of the causal agent, symptoms, host susceptibility, resistance durability and disease cycle.

Geographical distribution

Powdery mildew occurs wherever apples are grown. It can be both major and minor importance of the disease in commercial orchards but it is an important disease in apple nurseries worldwide (Hickey & Yoder, 1990). Economic loss dependent upon climatic conditions, cultivar susceptibility and orchard or nursery management practices. The management of powdery mildew in commercial orchards needs to be integrated with other apple diseases such as apple scab.

Taxonomy, causal organism and its morphology

Podosphaera genus within the *Erysiphaceae* family is commonly recognized as superficial mycelium, dichotomously

branched appendages at tip and chasmothecium (formerly cleistothecium) with one ascus (Salmon, 1900). The *Erysiphaceae* are called obligate parasites. On conventional media, such as potato dextrose agar, powdery mildew conidia may form short germ tubes with septa (Yossifovitch, 1923), but these germ tubes soon die.

Podosphaera leucotricha (Ell. & Ev.) E. S. Salmon (anamorph *Oidium farinosum* Cooke), an ascomycetous heterothallic fungus, causes powdery mildew of apple, pear and quince (Hickey & Yoder, 1990). Conidia (20–38 µm) are ellipsoidal and are produced on long chains on thin amphigenous mycelium. Chasmothecia are subglobose (75–96 µm in diameter) and have apical and basal appendages. The apical appendages (3 to 11 per chasmothecia) are brown basally and widely spreading; their length is 3 to 7 times the diameter of the chasmothecia. The apex is undivided once or twice dichotomously branched. The basal appendages are rudimentary, pale brown, and simple or irregularly branched. One ascus (55–70 × 44–50 µm) can be found in the chasmothecia, which are oblong to subglobose. Eight ovate to elliptical ascospores (22–36 × 12–15 µm) are found in the ascus (Hickey & Yoder, 1990).

Symptoms

The fungus attack twigs, foliage, blossoms and fruits. Infected twigs often are stunted and may die. When young leaves are infected, they tend to increase in length but not in width, and to become folded longitudinally (Ellis et al., 1981). Infections on leaves appear first on the lower surface. These lesions may spread to the upper surface and cover the entire leaf with a white spores and mycelium. Infections along the leaf margin often result in leaf curling or crinkling.

Severely infected leaves sometimes abscise by midseason. In nurseries, the fungus can spread to all developing leaves and cause severe stunting of vegetative terminal shoot (Hickey & Yoder, 1990).

Severely infected terminals have shortened internodes, and are covered with a silver-gray mycelium. The grayish white fungal growth turns brown, any many dark brown fruiting bodies appear (Hickey & Yoder, 1990). Infected terminal and buds are more susceptible to winter injury than healthy buds. Infected flower buds are also exhibit reduced fruit set. In the spring, infected flower buds open a few days later than healthy ones. Blossoms and first leaves can be covered with mycelium and spores. The petals are often change their colour, distorted and stunted (Hickey & Yoder, 1990).

Early fruit infection originated from diseased blossoms. Apple blossoms emerging from infected buds may give rise to small, russeted fruit. Infected fruits is covered with a network pattern of cork cells (Hickey & Yoder, 1990).

Host susceptibility and durability of resistance

One of the firts detailed studies on powdery mildew suceptibilities of apple cultivars were prepared by Aldwinckle (1974) and Norton (1981), which included all important cultivars form the US.

Borovinova (1982a) studied the susceptibility of 59 apple cultivars to powdery mildew in a multi-year study. Most cultivars were infested by powdery mildew, but to a different extent. Only cultivar Kolotny was very slightly susceptible with the degree of 1% disease incidence. Cultivars Linda, Gray Renette, Boiken, White Winter Kalvil, Rik's Renette, Renette des Grandes Villes, Beforest, Jonathan, Fenuette Grise, Fenuette Rouge, Wellington, Jonathan and Pepin Shafran were highly susceptible to powdery mildew with a disease incidence above 20%.

Borovinova (1982b) investigated the effect of the mineral fertilizers on the sensitivity of cv. Jonathan to powdery mildew. She found that the application of N, P₂O₅ and K₂O by 100, 40, 40 mg active ingredient per 1 kg dry soil, increased the sensitivity of Jonathan to powdery mildew.

According to Jeger *et al.* (1986) the association between the resistance components permitted resistance to be classified as very high for cv. Discovery, very low for cv. Golden Delicious or intermediate for cvs. Bramley's Seedling, Suntan.

According to Cimanowski *et al.* (1988), Liberty, Macfree, Paulared, Priam and Priscilla can be ranked as susceptible to apple powdery mildew, while the cultivars James Grieve, Prima, Redfree, Tydeman's Red are less susceptible to the disease.

Apple cultivars considered moderately to highly susceptible include Jonathan, Baldwin, Cortland, Idared, Rome Beauty, Monroe, Gravenstein, Stayman Winesap,

Cox's Orange Pippin, Granny Smith, and Prima. Less susceptible cultivars include Delicious, Golden Delicious, Winesap, York Imperial, Nittany and Lord Lambourbe (Hickey & Yoder, 1990).

Borovinova (1994) studied the susceptibility of scab resistant apple varieties to powdery mildew. All the evaluated varieties were susceptible to powdery mildew but to a different degree. Cultivar Moira was the most susceptible. According to her resarch, evaluated cultivars do not require any special control against powdery mildew.

Pedersen *et al.* (1994) studied the susceptibility of 15 apple cultivars to powdery mildew the results of which were compared with foundings of other researchers. All other works on powdery mildew suscpetibility of apple cultivars are partially summarized in Table 1.

Table 1: Sampled literature sources for susceptibility of some apple cultivars to *Podoshpaera leucotricha*

| Cultivar | Susceptibility to powdery mildew |
|------------------------|---|
| 'Belle de Boskoop' | Low (Mygind, 1965; Pedersen <i>et al.</i> , 1994; Cimanowski <i>et al.</i> , 1988) |
| 'Bramleys Seedling | Low (Mygind, 1963; Pedersen <i>et al.</i> , 1994; Jeger <i>et al.</i> , 1986; Norton, 1981) |
| 'Cox's Orange' | Medium (Pedersen <i>et al.</i> , 1994; Jeger <i>et al.</i> , 1986; Mygind, 1963), high (Jeger & Butt, 1983, 1986; van der Scheer, 1989; Hickey & Yoder, 1990) |
| 'Discovery' | Low (Pedersen <i>et al.</i> , 1994; Jeger & Butt, 1983, 1986; Jeger <i>et al.</i> , 1986; Norton, 1981; van der Scheer, 1989) |
| 'Elstar' | Medium (van der Scheer, 1989) |
| 'Filippa' | Low (Pedersen <i>et al.</i> , 1994; Mygind, 1963) |
| 'Gravenstein' | Low (Aldwinckle, 1974; Norton, 1981), medium (Pedersen <i>et al.</i> , 1994), high (Mygind, 1963; Hickey & Yoder, 1990) |
| 'Golden Delcicious' | Low (Jeger <i>et al.</i> , 1986; Hickey & Yoder, 1990) |
| 'Guldborg' | Medium (Pedersen <i>et al.</i> , 1994), high (Mygind, 1963) |
| 'Idared' | High (Hickey & Yoder, 1990) |
| 'Ildrod Pigeon' | High (Pedersen <i>et al.</i> , 1994; Norton, 1981) |
| 'Ingrid Marie' | Low (Pedersen <i>et al.</i> , 1994; low-medium (Mygind, 1963) |
| 'James Grieve' | Low (Pedersen <i>et al.</i> , 1994; Cimanowski <i>et al.</i> , 1988) |
| 'Jonathan' | High (Aldwinckle, 1974; Norton, 1981; Borovinova, 1982ab; Hickey & Yoder, 1990) |
| 'Jonagold' | Medium to high (van der Scheer, 1989) |
| 'Mutsu' | Low (Pedersen <i>et al.</i> , 1994; Norton, 1981), medium (Aldwinckle, 1974) |
| 'Moria' | Medium (Borovinova, 1994) |
| 'Prima' | High (Hickey & Yoder, 1990), low to medium (van der Scheer, 1989; Cimanowski <i>et al.</i> , 1988) |
| 'Red Ananas' | Low (Pedersen <i>et al.</i> , 1994) |
| 'Skovfoged' | Medium (Pedersen <i>et al.</i> , 1994) |
| 'Summerred' | Medium (Pedersen <i>et al.</i> , 1994; Aldwinckle, 1974; Norton, 1981; van der Scheer, 1989), |
| 'Transparente Blanche' | Medium (Pedersen <i>et al.</i> , 1994; Aldwinckle, 1974), high (Mygind, 1963) |

Selection for resistance to powdery mildew, caused by *P. leucotricha*, is based mainly on major resistance genes, which provide a high level of resistance (Lespinasse, 1983; Fischer, 1994; Krüger, 1994). Monogenic or oligogenic resistances have been identified in wild *Malus* species such as *Malus robusta* (*Pl1*), *Malus zumi* (*Pl2*) and Mildew Immune Selection (MIS), or in ornamental crab apples such as White Angel (*Plw*) and the D series (*Pld*) (Knight & Alston, 1968; Dayton, 1977; Visser & Verhaegh, 1979; Korban & Dayton, 1983; Gallott *et al.*, 1985). The use of cultivars carrying major resistance genes often results in a selection of virulent isolates in pathogen populations, which are able to overcome the resistance (Parisi *et al.*, 1993; Wolfe & McDermott, 1994; Lebeda & Zinkernagel, 2003). Resistance and its durability were widely investigated in France. The resistance from *M. zumi* were used mainly in the apple-breeding programme developed at the INRA in France. This resistance was initially considered to be the result of one dominant gene (Knight & Alston, 1968), but additional studies have shown that it might be more complex (Seglias & Gessler, 1997) and at least two genes may be involved (Alston, 1976). The source of resistance in *M. zumi* was considered to involve at least one single major resistance gene, named *Pl2*. The resistance introgressed from *M. zumi* was reported as stable under field conditions (Krüger, 1994), even over 17 years in unsprayed orchards (Alston, 1983). However, in later years in France, an increase of susceptibility to powdery mildew was observed on apple genotypes carrying *Pl2* gene (Caffier & Laurens, 2005). This increase of susceptibility could not be explained by tree age and/or by the amount of inoculum on expression of the resistance *Pl2* gene. It was demonstrated that that isolates of *P. leucotricha* sampled in this orchard were virulent to *Pl2* gene. Six years after planting of several apple genotypes with *Pl2* gene resulted in a breakdown of the resistance. Ten years after planting, the percentage of genotypes that were still resistant to powdery mildew varied between 2 and 56 % depending on the progenies. This suggested that additional quantitative resistance genes may influence the durability of resistance *Pl2* (Caffier & Laurens, 2005).

Disease cycle

P. leucotricha is an obligate parasite that overwinters as mycelium in dormant buds infected during the previous growing season (Woodward, 1927; Butt, 1971, 1972). Overwintering of the fungus is limited primarily by temperature. Infected buds are often failed to burst after a severe winters, The survival rate of these buds below -20°C is less than 5%, while healthy buds can survive the temperatures of -30°C (Covey, 1969). Temperatures below -12°C can kill the mycelium in the infected buds and allow the buds to produce healthy leaves (Hickey & Yoder, 1990).

At bud burst, conidia produced on overwintering mycelium in the infected bud, initiate the primary infections. These conidia infect young leaves, blossoms and fruit and provide inoculum for secondary disease cycles. Infections are regulated by temperatures and relative humidity. Young leaves are highly susceptible to the disease. At $10\text{--}25^{\circ}\text{C}$ (the optimum is $20\text{--}22^{\circ}\text{C}$) conidia can germinate between 4 and 30°C (the optimum is $20\text{--}22^{\circ}\text{C}$), the required relative humidity ranged between 70 to 100%. Germination is slow at temperatures below $4\text{--}10^{\circ}\text{C}$ and above $28\text{--}30^{\circ}\text{C}$ (Covey, 1968; Hickey & Yoder, 1990).

Fruit buds provide the earliest source of inoculum. Because infected buds usually open a few days later than healthy ones, susceptible tissue is already present when the first conidia are produced (Hickey & Yoder, 1990).

Production, dissemination and germination of conidia occur mainly during the light portion of the day (Yarwood, 1934; Burchill, 1965; Butt & Jeger, 1986). Maturation of conidia in *P. leucotricha* is also diurnal (Childs, 1940). The fungus releases spores with a diurnal periodicity, and the highest concentration of spores in the air occurs from midday to early afternoon (Hickey & Yoder, 1990; Xu *et al.*, 1995).

Cunningham (1923) indicates that the abundant chasmodectia play no part in the overwintering of the fungus. It is widely accepted that the sexual stage of *P. leucotricha* do not appear to be important in the disease cycle. Although germination during the winter months have been reported but attempts to germinate ascospores and/or to inoculate foliage with them have been unsuccessful (Hickey & Yoder, 1990)

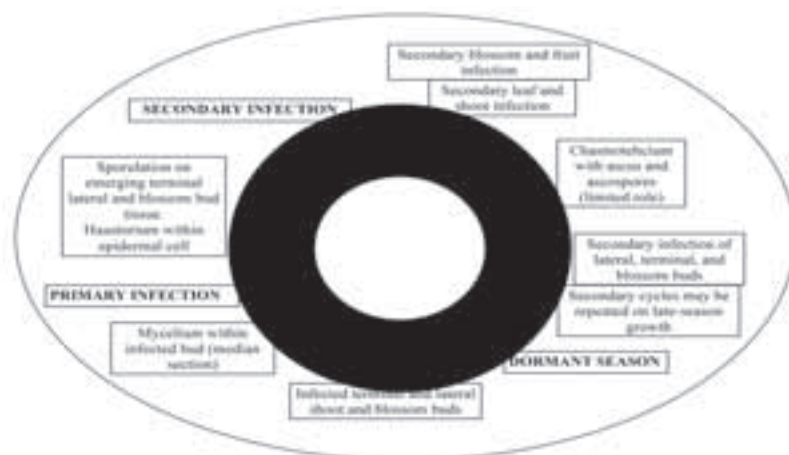


Figure 1: Disease cycle of *Podosphaera leucotricha*

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